THE CONSTANT POTENTIAL IN THE CEREBRAL CORTEX OF THE RABBIT

Zh. P. Shuranova

Laboratory of Electroencephalography (Scientific Director, Corresponding Member AN SSSR Professor M. N. Livanov), Institute of Higher Nervous Activity and Neurophysiology (Director, Corresponding Member AN SSSR É. A. Asratyan) of the AN SSSR, Moscow
(Presented by Active Member AMN SSSR N. I. Grashchenkov)
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The presence of a constant potential difference between the surface of the cerebral cortex and ventricles of the brain was first demonstrated by Libet and Gerard [3]. Many subsequent investigations have shown that the surface of the cortex has a small positive potential above that of various "indifferent" points (the nasal or occipital bone, the cervical muscles, the blood stream, etc.). Libet and Gerard put forward the hypothesis that the potential difference (called the "positive potential") is formed as a result of differences in the degree of polarization of the apical dendrites and the bodies of the pyramidal neurons of the cortex. This hypothesis is still regarded as most probable [4, 5]. It has been confirmed experimentally. N. A. Aladzhalova and O. Kh. Koshtoyants [1], in experiments on immobilized rabbits, showed that the deep layers of the cortex (at a depth of approximately 1.2 mm) are at a considerably more negative potential (10-15 mV) than the surface of the cortex. Frank [2] recorded a positive potential from the surface of an isolated strip of cortex in a cat, and a negative potential immediately below the surface. Meanwhile Tschirgi and Taylor [6] obtained no changes in potential when they inserted an electrode into the depth of various brain structures, including the cortex. They concluded that the constant background potential recorded from the surface of the cortex and its changes in different experimental conditions are mainly attributable to differences in the ionic composition on both sides of the blood-brain barrier, and that they bear little relationship to the functional activity of the neurons.

We have investigated the distribution of the constant potential along a vertical line in the sensorimotor and optic regions of the cerebral cortex in the rabbit.

EXPERIMENTAL METHOD

Experiments were performed on 35 rabbits weighing 2-3 kg; 67 experiments were carried out on animals anesthetized with Nembutal, 23 on animals immobilized with Diplacin and Tricuran. A few hours before the experiment, the rabbit's scalp was reflected and a burr-hole 5 mm in diameter made in the skull, usually over the sensorimotor or optic region, and occasionally over the parietal region. In some experiments several such holes (2-4) were made at the same time. After bleeding from the bone had ceased, the dura was removed with fine scissors. The vascular membrane was hardly ever injured during the course of this procedure. To avoid pulsation of the brain, a 1% solution of agar-agar was poured into the hole or a polythene ring, was lightly applied to the surface.

Potentials were picked up with calomel electrodes. The electrode (Fig. 1) consisted of a glass tube (diameter 14 mm, height 40 mm), into the bottom of which a platinum wire with a diameter of 0.3-0.5 mm was soldered. The tube was filled up in turn with mercury, calomel, and 7% NaCl solution. Through a hole in the stopper passed a connecting tube, terminating in a cotton wick. When not in use during the experiments, the electrodes were stored short-circuited in pairs in an exsiccator, with their ends dipped into 7% NaCl solution. Contact with the brain was made by means of a capillary tube filled with 0.9% NaCl solution; the diameter of the tip of the capillary tube varied in different experiments from 10 to 100μ (usually 20-40μ). During the experiment the electrodes and capillary tubes were fixed in special holders independently of each other, and the wicks were then lowered into the capillary tube. This method is sufficiently convenient and reliable.

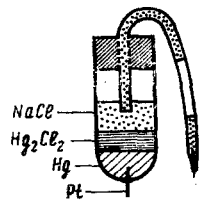

Fig. 1. Calomel electrode.

In most of the experiments to be described the active electrode was gradually (0.1 mm at a time) introduced deeper into the cortex by means of the micromanipulator of a stereotaxis apparatus. The capillary tube connected to the indifferent electrode (a second calomel half-cell) was placed deep in the nasal bone or in the fluid filling the burr-hole.

The potentials were recorded on a type UNI-1 apparatus for neurophysiological investigations (pass band 0-10 kc, maximal amplification 2 cm/100 μV, input impedance 1 MΩ) or on a type BÉKS-01 electrocardioscope (pass band 0-500 cps, maximal amplification 3 cm/mV, input impedance 1 MΩ); the screen was photographed by means of a Recordine camera. The drift of the amplifiers was small and of no practical significance, for the zero line was verified before each measurement. In some experiments a cathode repeater was used to increase the input impedance of the recording system.

EXPERIMENTAL RESULTS

An analysis was made of 90 cases of insertion of the electrode deep into the cortex. Despite the apparent dissimilarity between the results, a few principal groups can be distinguished among them. It was decided to exclude from the subsequent analysis the experiments in which the constant potential changed always in the same direction, for some form of instability of the recording system (the electrodes or the cathode repeater) was apparently present.

In 42 of the remaining 63 cases (67% defininite changes in the constant potential were observed as the electrode moved deeper, while in 21 cases (33%) there was no change in the constant potential when the electrode passed deeper into the cortex. In the latter group the constant potential most frequently remained slightly positive in relation to the indifferent point. On the other hand, in the experiments in which the constant potential changed as the electrode moved deeper into the cortex, this change took the form of a gradual increase in negativity in relation to the surface, reaching a maximum of negative potential, and thereafter declining. A graph plotted from the results of one of these experiments is shown in Fig. 2.

Analysis of the measurements taken at various depths in the sensorimotor and optic regions separately showed certain differences between the two. Statistical analysis of the results from which the curves in Fig. 3 were plotted shows that the zone where the negative potential reached its maximal value lay at a depth of 1.65 ± 0.07 mm in the sensorimotor region and of 1.2 ± 0.13 mm in the optic region ($P < 0.01$). The magnitude of the negative potential of this zone (in relation to the surface) was −2.5 ± 0.26 mV in the sensorimotor region and −1.6 ± 0.21 mV in the optic region ($P < 0.01$). Consequently, in the sensorimotor region the deep layers of the cortex evidently have a greater negative potential than those in the optic region; the zone of maximal negativity in the former is situated deeper than in the latter. It was interesting to note a tendency for two maxima of negativity to develop in the optic region. Unfortunately, it is too early to draw final conclusions because of the insufficient number of observations.

The results of these investigations agree partly with the findings of Tschirgi and Taylor and partly with those of N. A. Aladzhalova and O. Kh. Koshtoyants. Actually, in some experiments the constant potential did not change as the electrode passed deeper into the cortex; in most cases (67%), however, changes in the magnitude of the constant potential were found with changes in the depth of the electrode. We have no facts which could serve to explain these two groups of findings. The most interesting conclusion to be drawn at present is that statistically significant differences were established in the behavior of the constant potential in the two areas of the cortex investigated. More than the simple fact of the presence of changes in the constant potential with increasing depth into the cortex, this demonstrates its relationship to the concrete cortical structure. As might have been supposed from the cytoarchitectonic data, the maximum of negativity in the optic region was smaller in magnitude and less deeply situated than in the sensorimotor region.

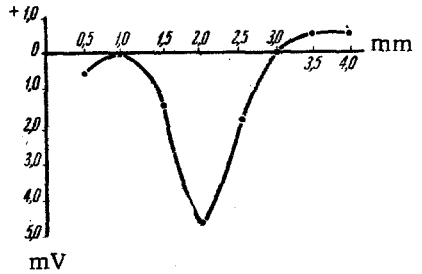

Fig. 2. Distribution of constant potential in sensorimotor region of cortex. Along the axis of abscissas – depth of electrode, along the axis of ordinates – potential difference between surface and different levels of cortex.

Comparison of the values of the maximal negativity and the depth at which they occur in our experiments with those obtained by N. A. Aladzhalova and O. Kh. Koshtoyants revealed certain differences. We cannot guarantee the absolute reliability of these figures because

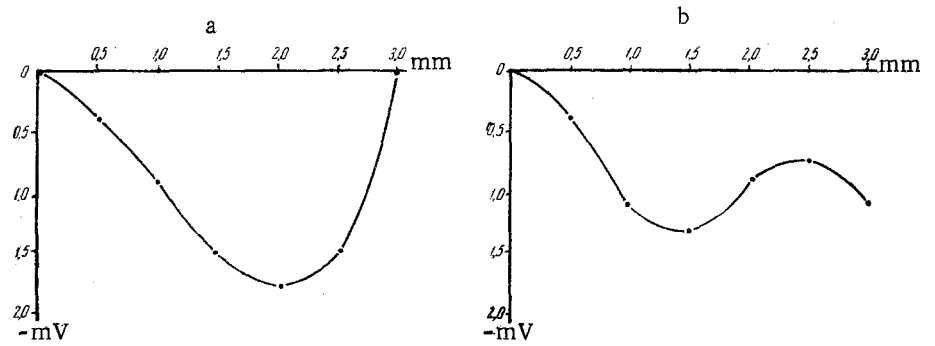

Fig. 3. Composite distribution curve of constant potential. a) In sensorimotor region; b) in optic region. Legend as in Fig. 2.

of unavoidable inaccuracies and of other factors for which it is difficult to make allowances in experiments of this nature. This applies above all to the determination of the depth of insertion of the electrode. For the most part several experiments were carried out on one rabbit on different days, so that morphological verification was very difficult, and the estimation of depth from the readings of the micromanipulator inevitably cannot be very accurate. The next factor complicating the picture is the functional state of the brain, depending on the individual peculiarities of the animal, the level of anesthesia, extraneous stimuli, the nature of the operation, and so on. Furthermore, in experiments in which the electrode is gradually implanted deeper and deeper, some allowance must be made for the injury potential, which may evidently differ in its magnitude and in its course over a period of time at different depths in the cortex. It seems that the most reliable results may be obtained from experiments in which one or several electrodes are buried in the cortex for long periods of time. Experiments along these lines are being carried out by us at the present time.

SUMMARY

The constant potential of superficial and deep layers of cerebral cortex were recorded with the aid of calomel electrodes and a d.c. amplifier in anesthetized (nembutal) and immobilized (diplacin, tricuran) rabbits. In 33% of cases no changes of the constant potentials were observed when burying the electrode; in 67% of cases deep layers were negative with respect to the surface. In the sensorimotor area deep cortical layers had a greater negative potential than in the optic area; the zone of maximal negativity in the sensorimotor area was located deeper than in the optic area.

LITERATURE CITED

1. N. A. Aladzhalova and O. Kh. Koshtoyants, Biofizika, 3, 327 (1957).
2. G. B. Frank, Proc. (1958), 17, 1, part 1, p. 48.
3. B. Libet and R. W. Gerard, J. Neurophysiol. (1941), 4, 438.
4. B. Libet and R. W. Gerard, Electroenceph. clin. Neurophysiol. (1962), 14, 445.
5. W. H. Marshall, Physiol. Rev. (1959), 39, 239.
6. R. O. Tschirgi and J. L. Taylor, Am. J. Physiol (1958), 195, 7.

All abbreviations of periodicals in the above bibliography are letter-by-letter transliterations of the abbreviations as given in the original Russian journal. *Some or all of this periodical literature may well be available in English translation.* A complete list of the cover-to-cover English translations appears at the back of this issue.
